THE BIOLOGY OF PSEUDOCALANUS MINUTUS IN THE GULF OF MAINE AND BAY OF FUNDY

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Introduction

The present paper forms the second of a series on the biology of zoöplankton species in the Gulf of Maine and Bay of Fundy, with special reference to production and dispersal. As in the case of *Calanus finmarchicus* (Fish, 1936) there have been two objectives; first, a determination of breeding seasons, annual number of broods, and rate of growth; second, an evaluation of different spawning areas and dispersal of eggs and larvæ. For a description of the area covered, location of stations and methods, the reader is referred to the aforementioned report. The studies were carried on between July 28, 1931 and September 29, 1932 for the International Passamaquoddy Fisheries Commission.

Regional Distribution of the Adult Stock[2]

Pseudocalanus minutus was found by Bigelow (1926, pp. 276–277) to be nearly as universal as *Calanus* in the Gulf of Maine, distributed indifferently in the coastal zone, the deeper parts of the basin, and on offshore banks. It was somewhat more nearly universal close along shore but the numbers actually present averaged larger in the basin, entrant channels, and along the offshore slope. In 1931 and 1932 it was found generally distributed in both neritic and offshore waters.

Being more indifferent to neritic environmental factors than *Calanus* and with an apparently somewhat greater thermal range, *Pseudocalanus* occurs to some extent throughout the year in inshore waters north of Cape Cod. However, like other boreal arctic species, its numbers decline rapidly with rising summer temperatures in shallow areas, and offshore Bigelow (Ibid., p. 277) observed that there is a general tendency to leave the uppermost stratum in April and May.

In Passamaquoddy Bay in 1932 there was a decline in the relative percentage of *Pseudocalanus* from 84.7 per cent on June 20 to 2.8 per cent on July 30, with a corresponding reduction in the volume of plankton from 26.7 cc. to 1.9 cc. Later it rose again to 12.1 per cent ac-

[1] Contribution No. 94.

[2] "Adult stock" includes late copepodites (for the most part stage V) appearing in the coarse net hauls.

companied by an increase in volume to 13.3 cc. on September 23. McMurrich's unpublished data from St. Andrews in 1916 accord with these results.

In Frenchmans Bay, *Pseudocalanus* remains throughout the summer as one of the most important members of the zoöplankton community in the cold bottom water, but its center of abundance was found by day at a slightly higher and warmer level than that of *Calanus*.

South of Cape Cod *Pseudocalanus* largely disappears from the neritic zone during the summer months. In the Woods Hole region it remains abundant until May, declines rapidly in June after the water mass rises above 15° C., and disappears at about 20° C., reappearing usually in October (Fish, 1925, Fig. 45). *Calanus* occurs only during the coldest months in this area and is rarely ever numerous. Farther south in Chesapeake Bay *Pseudocalanus* is regularly found in the inner bay in the spring, but *Calanus* appears to be confined to the outer bay, where it is taken only in winter (Wilson, 1932, p. 13).

It would appear, therefore, that *Pseudocalanus* regularly outnumbers *Calanus* in observed neritic localities south of Cape Cod, and north of the Cape a similar condition occurs occasionally in some coastal areas during the early summer.

Production and Dispersal of Eggs and Larvæ

Spawning Areas

The distribution of eggs and early nauplii in 1931 and 1932 indicates that *P. minutus* spawns throughout the Gulf and Bay of Fundy. Even in neritic areas such as Passamaquoddy Bay where no evidence of *Calanus* propagation was found, 2,847 *Pseudocalanus* eggs per minute were taken on June 20, and 760 per cubic meter at the end of July in 1932.[3]

There is, however, considerable variation in the extent of propagation in different parts of the region. If the *Pseudocalanus* population in the inner Gulf and Bay originated largely in the western coastal area, as appears to be the case with *Calanus*, one would expect the quantitative distribution of larvæ of the two species to be very similar. The data obtained in 1932 indicate striking differences. Whereas the numbers of *C. finmarchicus* in all stages declined uniformly to the eastward (Fish, 1936, Fig. 11) and quantitative fluctuations in the western area were reflected throughout the region, in *P. minutus* the number of larvæ in the eastern basin and particularly in the outer part of the Bay

[3] Just outside of the bay in outer Quoddy waters (Sta. 5) *Calanus* eggs totalled 7,608 per minute and *Pseudocalanus* 37,018 on June 20, and *Calanus* 710 per cubic meter and *Pseudocalanus* 800 on July 30.

of Fundy was usually as large or even larger than west of Mt. Desert (Fig. 1).

This condition could have resulted either from intensive local spawning or large contributions from other areas. In regard to the first possibility, evidence of immigration in the horizontal distribution of all advanced larval stages of *P. minutus* indicates that production of this species in the eastern coastal region is on the whole probably no more successful than that of *C. finmarchicus* (Ibid., p. 140), *Sagitta elegans* (Huntsman and Reid, 1921, p. 110), and fishes having pelagic eggs (Bigelow, 1926, pp. 70–73; Huntsman, 1918, p. 65, 1922). Considering other possible sources of supply, as propagation in the western coastal area does not seem to have been sufficient to account for the in-

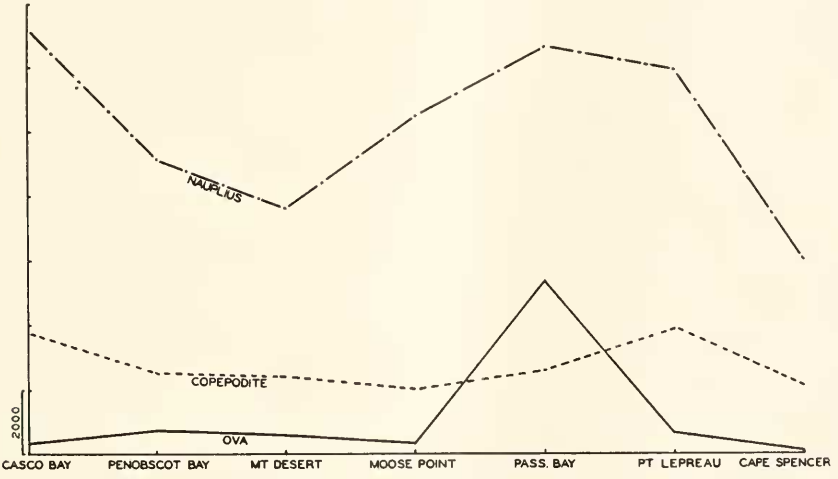

FIG. 1. Mean numbers of ova, nauplius and copepodite stages of *P. minutus* per minute of towing for the period April–July, 1932.

creasingly large numbers of *Pseudocalanus* occurring farther east (up to 215,698 late nauplii per minute in the Bay of Fundy in June) as the season advanced (Fig. 7*B*), it is probable that the principle spawning area of *P. minutus* is located in the outer Gulf where Bigelow (1926, p. 277) regularly found the species most abundant. The western coastal area appeared to be an important source for the first brood (Fig. 5*A*) in 1932, but thereafter declined until in mid-August there was little evidence of appreciable propagation except in a restricted locality represented by the innermost stations between Casco and Penobscot Bays (Figs. 8*A* and *B*).

Breeding Seasons

The breeding periods of *P. minutus* appear to be somewhat similar

to those of *C. finmarchicus*. As in the latter species, propagation begins earlier in the southern portion of its range and there appear to be a greater number of annual broods.

South of Cape Cod *Pseudocalanus* enters neritic waters in late October and breeding must soon follow because in 1922–23 early copepodite stages appeared at Woods Hole by the middle of December (Fish, 1925, p. 144). A maximum of copepodites in January was followed by a rise of adults in February. A second brood of less importance appeared in March and April. Some no doubt enter the region from the north where vernal augmentation takes place at this time, but in view of the abundance of adults at Woods Hole in February, it seems probable that the greater part of the March–April copepodites were of local origin. With the rise in temperature in May the numbers declined, and the species practically disappeared from inshore waters in June. Subsequent broods no doubt occur offshore where *Pseudocalanus* is found throughout the summer. The southern limit of successful propagation is not known but its presence regularly in Chesapeake Bay in winter and spring (Wilson, 1932) would suggest that there may be some successful spawning at that latitude during the cold months.

North of Cape Cod, Willey (1918, p. 187) reported females with eggs and attached spermatophores in August, and Bigelow (1926, p. 282) concluded that "the seasonal fluctuations in the numerical strength of the stock point to breeding as taking place most actively from June until September and to the entire gulf as its site."

Ruud's records (1929, pp. 67–68) indicate that the cycle in Norwegian waters is somewhat similar to that of *C. finmarchicus*. Spawning begins in March off Möre and probably earlier off the west coast of Norway. In 1926 there was a maximum of copepodite stages I–III on April 28–29. All copepodite stages had another maximum on July 20. This would suggest production in March, the young reaching maturity in May–June and the second generation attaining copepodite stages by July 20. Several observers have reported the presence of copepodite stages and mature adults in northern waters during the summer (Störmer, 1929, p. 31; With, 1915, p. 61; Bogorov, 1932).

In the Gulf of Maine and Bay of Fundy the seasonal distribution of young stages in 1931 and 1932 indicates that propagation begins in March and continues in a succession of generations throughout the region until September.

Regional variation.—Eggs of *P. minutus* appear at progressively later periods in the outer Gulf, western area, and Bay of Fundy, and, on the basis of this regional variation in the time of spawning, it is possible to distinguish three major breeding stocks.

These stocks are not permanently restricted to their respective localities, but merely represent delayed maturation of that portion of the winter population of *P. minutus* which happens to be located in the eastern part of the Gulf and Bay of Fundy during the spring, and earlier maturation in areas to the westward where the water mass responds more rapidly to vernal warming.[4] This is evident from the fact that the progeny of all stocks disperse and appear to become established over much if not all of the region, and also because within a region with a dominant drift it would be impossible to have permanently localized zoöplankton stocks without bottom stages. From the surface to the bottom the plankton population in any part of the open Gulf and Bay is in varying degrees a transient one. However, since the annual cycle in the three major areas starts at different times, with approximately the same interval of development (p. 200), one would expect the distinct breeding periods of the three stocks to be continued, as in *Calanus* (Fish, 1936, p. 130), in subsequent generations no matter where they might be dispersed. This is indicated in the present material.

In the following pages symbols will be used to designate the different stocks originating in the three general regions in the spring, and their respective progeny wherever distributed during the remainder of the season: *A* indicating the outer gulf stock, *B* that of the western coastal area, and *C*, that originating east of Mt. Desert in the inner Gulf and centered in the Bay of Fundy.

Annual Cycle in Different Breeding Stocks

Tracing the succession of broods in the three breeding stocks of *P. minutus* is more complicated than in *C. finmarchicus*. Unlike the latter species, where the bulk of the population of the Gulf apparently originates in one area (western) and can easily be traced, the broods of *P. minutus* are everywhere so largely depleted before copepodite stages are reached, that the particular stock which happens to be in early larval stages at the time dominates throughout the Gulf and Bay. Copepodite stages were almost always relatively sparse and in the present collections rarely formed appreciable maxima.

Since the succession of generations is most clearly defined in the stock maturing in the western coastal region in the spring, this stock (*B*) will be considered first. There appear to be at least three and possibly four breeding periods: March–April, May–June, July–August, and September. As seen in the quantitative distribution in successive

[4] It is probable that the transfer of adults from one area to another is relatively much slower than that of larvæ because, by descending during the daylight hours, they pass beyond the influence of the surface into a slower dominant drift.

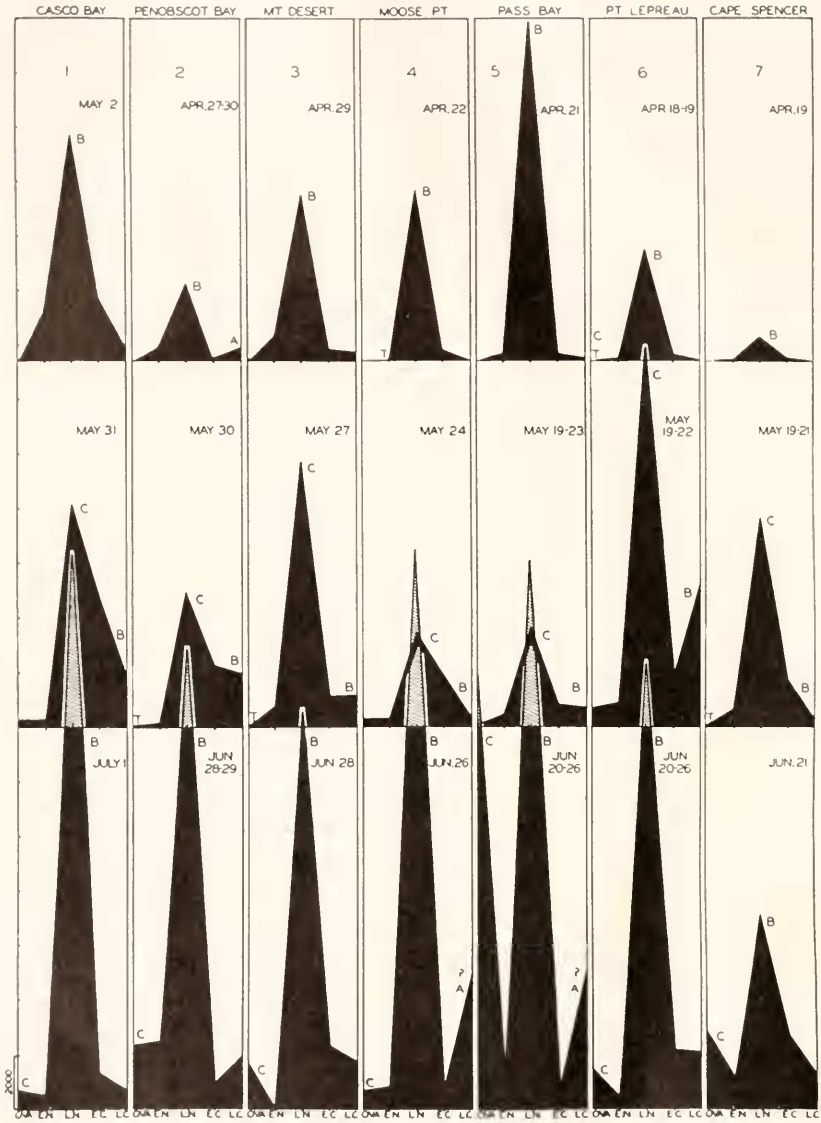

FIG. 2. Changes in the composition of the population of *Pseudocalanus minutus* (developmental stages) in seven sections between Casco Bay and Cape Spencer from April to June, 1932. Number per minute of towing. Stages recorded as: ova, early nauplii (I–III), late nauplii (IV–VI), early copepodites (I–III), and late copepodites (IV–V). *B* indicates stock originating in the western area in the spring, *C* indicates that of the eastern Gulf and Bay of Fundy, and *A*, the outer Gulf stock. *T*—trace.

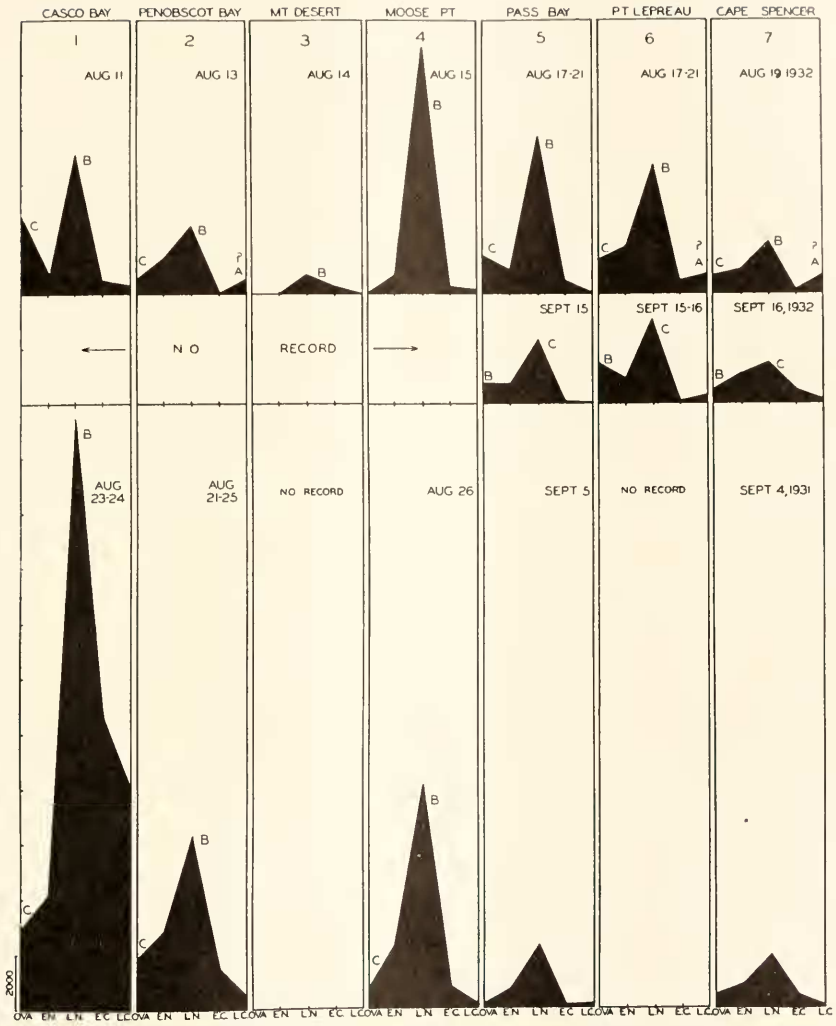

FIG. 3. Composition of the population of *Pseudocalanus minutus* (developmental stages) in August and September, 1931 and 1932. Number per cubic meter. Stages and symbols as in Fig. 2.

months, the first brood in advanced nauplius stages in late April had reached late copepodite stages on May 19–22 (Fig. 2, Section 6), and mainly completed the final moult by May 31 (Section 1). What is assumed to have been the second and largest western brood was represented by a maximum of late nauplius stages in the latter part of June. It would thus appear that the cycle during the early season is completed in about 60 days. The third brood, hatching on July 30 (Fig. 4), prob-

ably developed somewhat more rapidly with warmer summer temperatures and attained late nauplius stages by mid-August in the western area (Fig. 3). Even in the eastern Gulf at lower temperatures a large part of this stock passed from early to late nauplius stages between August 8 and 15, as indicated in Table I. Eggs entering the Bay of Fundy on

TABLE I

Stage	August 8, Sta. 15	August 15, Sta. 33
Egg	1,132	
Early nauplius	4,335	565
Late nauplius	5,842	12,060
Early copepodite	1,695	565
Late copepodite	377	377

September 15–16 would suggest a fourth generation but further data from the Gulf at this season are needed. It seems probable that a considerable percentage of the third crop remains in late copepodite stages to form the winter stock.

In stock C, originating in the eastern area, there is evidence of three breeding periods: April–May, June–July, and August. Local propagation was just beginning in the Bay of Fundy on April 19 (Fig. 2, Section 6) and a month later nauplius stages dominated. With a cycle of 60 days, eggs on June 20 (Fig. 4) would represent a second brood which by August 11–21 had matured and were spawning (Figs. 3 and 8*A–B*). A third brood is indicated by a maximum of late nauplius stages in the Bay of Fundy on September 15 in 1931 (Fig. 4), and September 15–16 in 1932 (Fig. 3).

Some less definite indications of a possible succession of generations in stock *A* after April are to be found in the data from the coastal region and the Bay.[5] In 1932, on June 20–26, when stock *B* was mainly in late nauplius stages, and the second brood of eggs of stock *C* had just appeared, a smaller maximum of late copepodite stages (Fig. 2, Sections 4 and 5) in the eastern basin may have represented a second brood of immigrants from offshore (Fig. 9*A*). With a developmental period of two months this would be expected. There is also an indication of a third crop of late copepodites on August 11–21, particularly in the western area (Fig. 3, Section 2) and the Bay of Fundy (Sections 6 and 7), but the numbers are too small to be of any real significance (Fig. 9*B*).

Although there was no detectable trace of stock *A* in May (Fig. 2), on the basis of the developmental period, the succession of subsequent maxima just described would appear reasonably indicative were it not

[5] In *Calanus*, either spawning in the outer gulf and western area coincides or the number of individuals of the offshore stock is insufficient to exert a detectable effect on the larval population of the inner gulf and bay.

for another complicating factor—the relatively small numbers of progeny attributable to this stock. There appears to be no logical reason for the depletion of one breeding stock of *Pseudocalanus* and the survival of another in the same locality. It is probable, therefore, that following the first generation of stock *A*, due to overlapping spawning periods, subsequent broods of this stock and stock *C* cannot with certainty be distinguished. At least a part of stock *A*, in copepodite stages

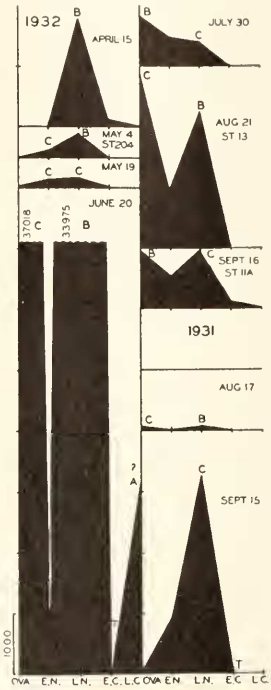

FIG. 4. Composition of the population of *P. minutus* in developmental stages at Station 5 (unless otherwise noted) in the New Brunswick area of the Bay of Fundy, showing the succession of generations of the (*B*) western, (*C*) eastern, and (*A*) outer Gulf stocks. *T* indicates trace. April–June: number per minute. July–September: number per cubic meter.

in the outer Gulf on April 11–12 (Fig. 5*B*), would be expected to have matured and started to spawn by the time eggs, forming the first brood of stock *C*, appeared in the Fundy region in the latter part of the month. In this case subsequent maxima, appearing in each instance one month after maxima of similar stages of stock *B*, would represent the combined stocks *A* and *C*, and the maxima of late copepodite stages [6] in late

[6] These copepodites, according to this interpretation, were probably derived from eggs appearing near the end of the previous spawning period and might be indicative of either one or both stocks.

June and August should be grouped with eggs appearing at the time. Further evidence in support of this contention will be presented later (pp. 209–211). In any event, with a similar rate of growth, it is reasonable to conclude that in stock *A* there are four broods, each of which appears about a month earlier than in stock *B* and two months or approximately one generation in advance of stock *C*.

Annual variation.—Observations at corresponding stations were made approximately two weeks later in 1931 than in 1932. As in the case of *Calanus* (Fish, 1936, p. 130) the season appeared about equally advanced in the western area, the slight increase in the percentage of copepodite stages off Casco Bay in 1931 (12 days later) being expected (Fig. 3).

In the central area east of Mt. Desert, and the Bay of Fundy, the fact that the relative numbers in comparable stages were approximately the same in the two years, would indicate that in 1931 the season was delayed about two weeks, a condition also according with *Calanus* (Ibid., p. 130).

TABLE II

Stage	Central Area		Bay of Fundy	
	1931 (Aug. 26)	1932 (Aug. 8–15)	1931 (Sept. 1–5)	1932 (Aug. 17–21)
Egg	750	566	225	1,041
Early nauplius	2,204	1,414	800	1,091
Late nauplius	8,117	8,810	2,937	4,112
Early copepodite	799	989	275	302
Late copepodite	188	330	112	442

Mortality in Developing Larvæ

The degree of mortality in developing larvæ of *P. minutus* can best be seen by comparing the relative abundance of different stages with those of *C. finmarchicus*. Of the two species *Pseudocalanus* must be by far the more prolific. The large number of spermatophores frequently found attached to individual females (Willey, 1919, p. 187, records as many as 24) suggests high egg production. The ovisac when attached contains usually from one to three eggs, but this may prove to be an adaptation for temporarily retaining the eggs to insure fertilization. Sars (1903, p. 21) observed that the sac is so fragile that it easily becomes detached at the slightest touch, and in examining Bigelow's collections (1926, p. 281) taken throughout the period of propagation in the Gulf of Maine, Wilson failed to find a single egg-bearing

female. Individuals with from one to two attached eggs were frequently taken in 1932, but to account for the numbers of free eggs of this species present at times in the region, several hundred must be produced by each individual. During the season of 1932, as shown in Table III,

TABLE III

1932	Eggs and young (all stages)		Relative percentage of adults	
Month	P. minutus	C. finmarchicus	P. minutus	C. finmarchicus
April	7,126	2,011	12.4	25.7
May	11,610	7,454	12.7	56.4
June	24,967	10,588	16.8	44.7
August	6,435	3,135	2.1	35.6
September	4,378	794	1.3	37.3

April–June: number per minute. August–September: number per cubic meter. Relative percentage of adults (including stage V) in the zoöplankton population.

although adults (including stage V) were outnumbered by *Calanus* in the total region by an average ratio of over 4 to 1, eggs and larvæ of *Pseudocalanus* dominated at all times with an average ratio of 2.5 to 1.

TABLE IV

Section	1932	P. minutus	C. finmarchicus
Casco Bay	April–June	17,248	13,137
	August	8,049	4,466
Penobscot Bay	April–June	12,442	9,490
	August	4,897	4,342
Mt. Desert	April–June	13,635	7,160
	August	956	1,860
Moose Peak	April–June	12,834	3,679
	August	10,181	5,184
Passamaquoddy Bay	April–June	20,494	4,749
	August–September	6,072	2,145
Pt. Lipreau	April–June	16,424	6,873
	August–September	7,164	1,516
Cape Spencer	April–June	8,893	1,665
	August–September	3,813	578

April–June: number per minute. August–September: number per cubic meter.

This is seen in Table IV to occur everywhere in the inner Gulf and Bay, the differences being greatest east of Mt. Desert.

Unlike *Calanus,* in which the depletion appears to be most extreme following the final moult (Nicholls, 1933, p. 95; Fish, 1936, p. 136), the decline in *Pseudocalanus* seems to be greatest in late nauplius stages.

There must also be a second critical period during maturation, which affects a far greater percentage of the stock than in *Calanus*, to establish the adult ratio because copepodite stages of *Pseudocalanus* exceeded those of Calanus during both the early and late summer seasons. (See Table V.)

Physical environmental factors appear to offer no logical cause for the depletion throughout the Gulf and Bay, and in the case of the late nauplii it seems to be attributable to destruction by enemies. Were there a lack of food, the relative decline in *Calanus* and *Pseudocalanus* larvæ would be expected to be similar.

Dispersal and Result on Regional Abundance of the Stock

The dispersal of eggs and larvæ from production centers and subsequent distribution of the adult stock are largely dependent on non-tidal circulation. The surface drift in the Gulf of Maine is counter-clock-

TABLE V

Total region 1932	April–June (Mean number per minute)		August–September (Mean number per cubic meter)	
Stage	P. minutus	C. finmarchicus	P. minutus	C. finmarchicus
Nauplius	10,568	2,160	4,476	638
Early copepodite	1,468	1,103	230	48
Late copepodite	1,079	514	292	10

wise, eddying around a central vortex. Eggs and larvæ produced in the western area would tend to be transported offshore and eastward around the outer margin of the Gulf. Outflow around the eastern end of Georges Bank as well as past Cape Cod would carry some of the larvæ, particularly those near the periphery of the drift, out of the region. However, an appreciable portion of the migrant stock or its progeny would be expected to remain within the Gulf completing the circuit across the entrance of the Bay of Fundy and westward along the coast of Maine, and some would continue eastward into the Bay along the Nova Scotian side.

One would therefore expect to find larvæ from the western area circling the outer Gulf and, with contributions from the latter area, supplementing the stock in the eastern basin and Bay of Fundy. Similarly, the greater number of eggs and larvæ originating in or entering the Fundy region would, if they survived, leave the Bay in the outflow which passes east and south of Grand Manan and tend to be dispersed westward in the inner gulf.

Dispersal in 1932.—Dispersal of individual stocks through successive generations has been traced by the monthly changes in the distribution of larvæ. Although stages ranging from ova to adults could usually be found almost everywhere in the region at any time, the maximum numbers, particularly of stock *B*, were in stages sufficiently separated from those of the other stocks to permit detection (Figs. 2 and 3).

Stock B.—Late nauplius stages, representing the first brood of that portion of the *P. minutus* population located in the western Gulf in the spring, were widely distributed throughout the region with local concentrations in the western and eastern basins by late April (Fig. 5*A*). A considerable part of the parent stock must have been transported well around the outer Gulf before spawning to account for such large numbers of nauplii in the Fundy region. There is a possibility, of course, that the larvæ might have been locally produced, but the sparseness of earlier stages east of Mt. Desert in the inner Gulf (Figs. 2 and 3) at this time and the appearance later of a distinct eastern brood (p. 200) warrants the conclusion that they were derived from parents transported from the western Gulf.

The concentration of late nauplii in a limited area off Halifax (Fig. 5*A*) indicates that the season, as in the case of *Calanus* (Fish, 1936), was as far advanced there as in the western coastal region. In the intervening region late nauplii were not found numerous until May, a condition somewhat comparable with the Bay of Fundy.

From April to May stock *B* declined greatly in numbers and by the time late copepodite stages were reached at the end of the latter month, quantities in excess of 1,000 per minute were found only in the inner Gulf west of Mt. Desert and over the central basin of the Bay of Fundy (Fig. 6*C*). The latter were no doubt migrants from the western or outer Gulf because copepodites were still very sparse as far west as Mt. Desert in the path of the outflow from the Bay, where one would have expected to find the stock present in the Fundy region in April if it had survived.

By the end of June important changes in the picture were noticeable. The second brood of stock *B* in late nauplius stages was, like the first brood in May, centered in the western coastal area and Bay of Fundy. In view of evidence of unsuccessful production in the latter area (p. 195), and the large number (21,410) of late nauplii in the entering drift on the Nova Scotian side, it seems probable that the April brood of stock *B* had become established in the general region of Georges Bank and the second brood of migrant larvæ from the western area were now being supplemented by increasingly large contributions from the outer Gulf. It was at this time (June 21) that the immense swarm mentioned on page 195 was encountered off St. John (Fig. 7*B*).

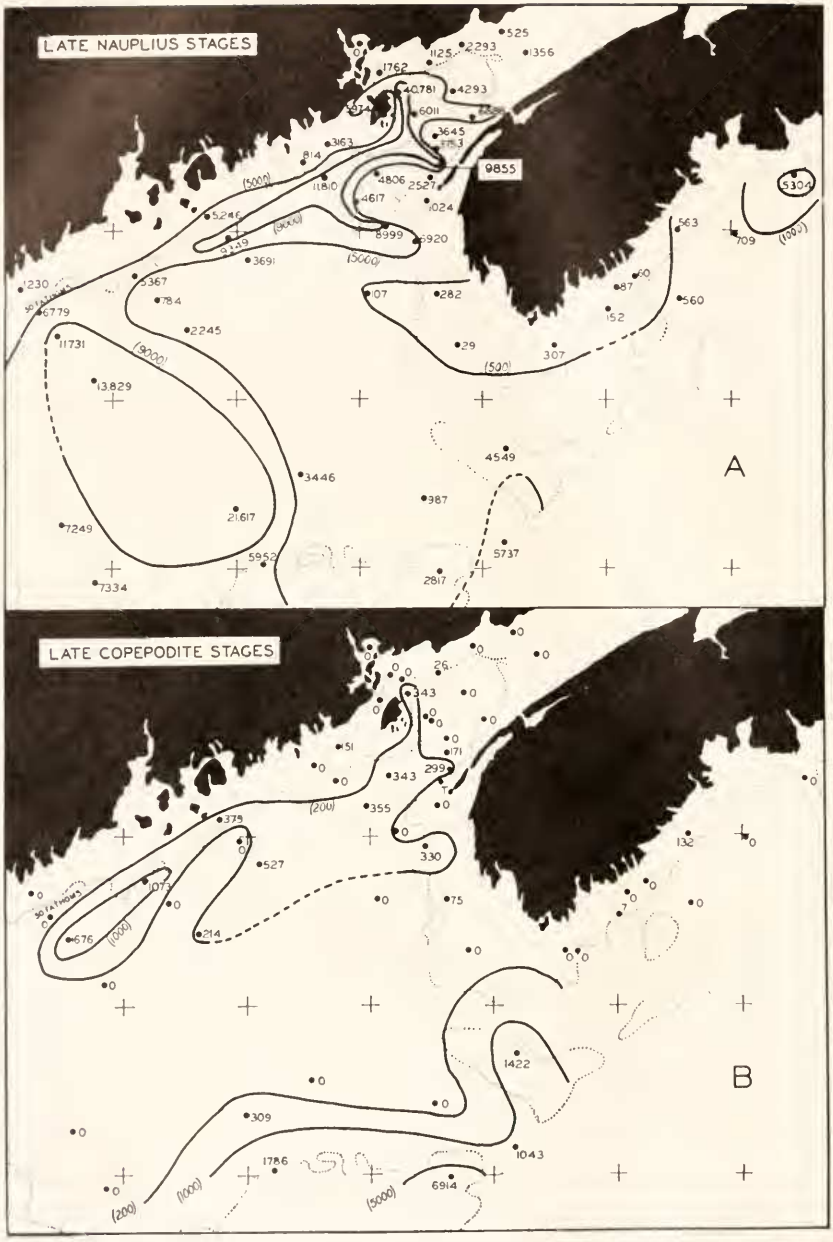

FIG. 5. Occurrence of late nauplius stages (*A*) of the western stock, and late copepodite stages (*B*) considered indicative of offshore propagation, in April, 1932. Number per minute of towing.

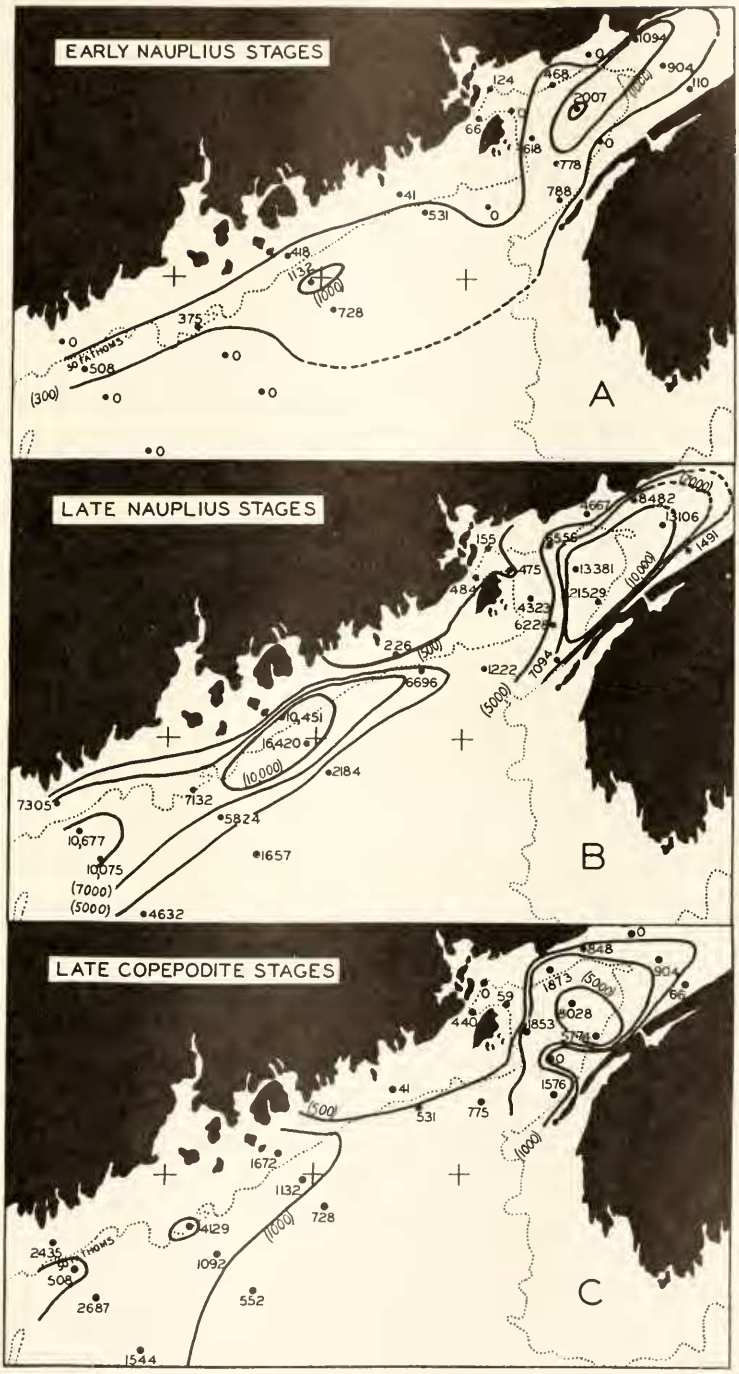

FIG. 6. Occurrence of nauplius stages (*A–B*) of the eastern stock, and late copepodite stages (*C*) of the western stock in May, 1932. Number per minute of towing.

There can be no doubt that by mid-August the larger part of the *P. minutus* population was originating in offshore waters. The third brood of stock *B*, by this time in late nauplius stages (Figs. 3 and 4), was, in the inner Gulf, definitely centered in the eastern basin and along the Nova Scotian side of the Bay of Fundy (Fig. 8C). Immigration of this population from the outer Gulf is indicated by the continued scarcity of larvæ in the New Brunswick area and the coastal zone of

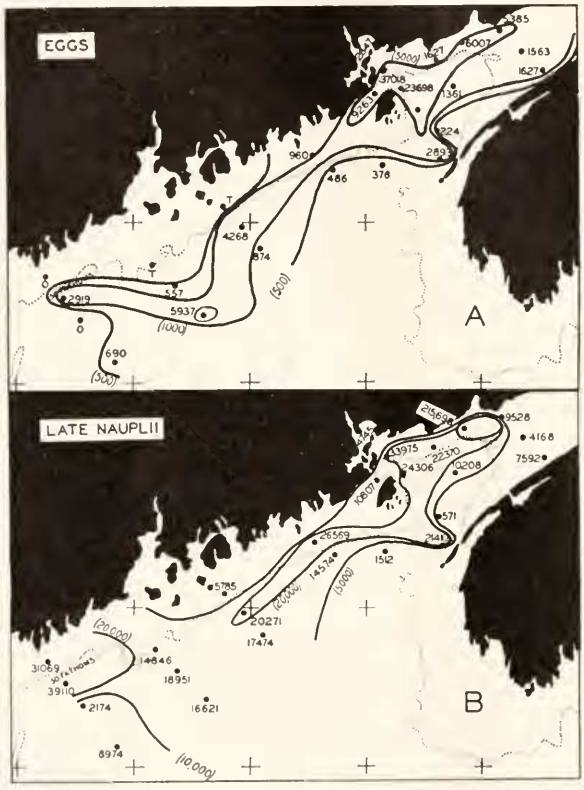

FIG. 7. Occurrence of eggs (*A*) of the second eastern brood and late nauplii (*B*) of the second western brood in June, 1932. Number per minute of towing.

eastern Maine beyond the immediate influence of the drift. The stock in the western area had declined until only at the innermost station off Casco Bay were more than 5,000 late nauplii per cubic meter taken.[7] If these conditions can be considered normal, then once the first brood of the stock originating in the western area in April becomes dispersed throughout the region, a considerable portion of the second brood, and

[7] Possibly the large population of predatory plankton animals in this region in summer depletes the *P. minutus* larval stock.

the greater part of the third, are derived from individuals establishing themselves in the general region of Georges Bank.

Autumn dispersal in the Gulf could not be traced as observations were restricted to the Bay of Fundy after August. By September both eggs (presumably the fourth brood of stock *B*) and larvæ of *P. minutus* had declined greatly in the Bay.

Stock C.—Originating from that portion of the *P. minutus* winter population maturing in the eastern Gulf and Bay of Fundy, stock *C* is believed to have been represented by small numbers of eggs at Station 37 in the Bay on April 20. Vernal augmentation must have just begun because eggs were not found elsewhere in April.

Differing from stock *B*, in which maturing adults of the parent stock had apparently become widely dispersed in the Gulf before spawning (Fig. 5*A*), propagation of the first brood of stock *C* seems to have been largely if not entirely restricted east of Mt. Desert. By May 18–24, late season eggs were not found outside of the Bay of Fundy;[8] early larvæ occurred at but two out of seven stations in the western area (Fig. 6*A*), and late nauplius stages (Fig. 6*B*), although more widely dispersed, were centered in the Bay of Fundy and along the course of the coastal drift from the eastward. It is probable that these late nauplii originated in the eastern basin and not in the Bay of Fundy because in the latter area the largest numbers were found in the course of the entering drift. Indicating local conditions beyond the immediate influence of this inflow, there was little evidence of survival in New Brunswick and eastern Maine coastal waters (Fig. 6*B*).

An analysis of the dispersal and resulting regional abundance of subsequent generations of this stock is rather complicated. Apparently the large numbers of late nauplii entering the western area in May (Fig. 6*B*) failed to establish themselves, for when this brood matured and were spawning in late June (Fig. 2) the numbers of eggs everywhere west of Mt. Desert were relatively small and at several of the stations none were found (Fig. 7*A*). This may have been due to destruction by enemies as previously suggested (p. 208) because the rich local population of plankton animals was at its maximum, and, as shown by conditions in August (Fig. 8), all of the breeding stocks of *P. minutus* were rapidly depleted in that area. On the other hand, corresponding to this decline in the western Gulf, there was a surprising increase of adults and eggs in the Bay of Fundy in late June. In the New Brunswick area adult *P. minutus* formed up to 83.2 per cent of the total zoöplankton population (Table VI, p. 213) and eggs up to 33,975 per

[8] Eggs, up to 1,405 per minute on May 19, were found only along the New Brunswick coast where the season appeared more retarded than elsewhere in the eastern region.

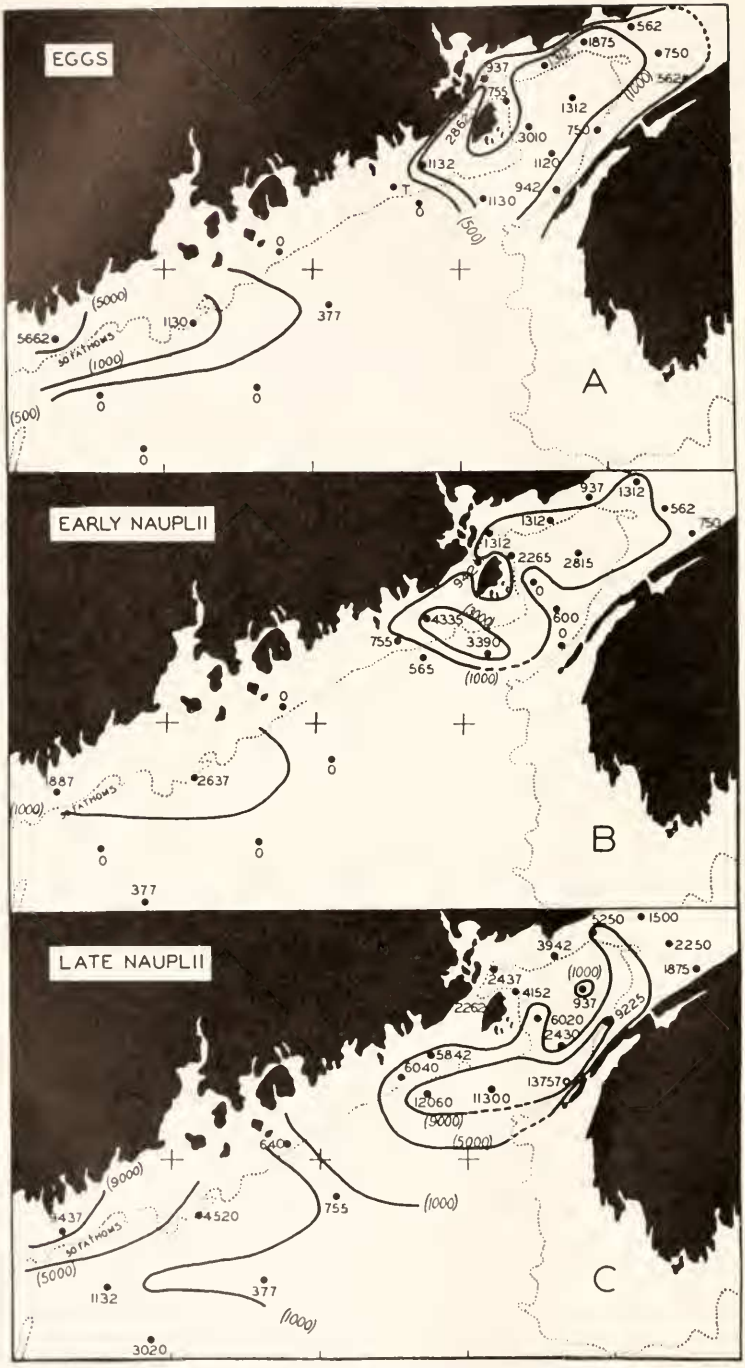

FIG. 8. Occurrence of eggs and early nauplii (*A–B*) of the third eastern brood and late nauplii (*C*) of the third western brood in August, 1932. Number per cubic meter.

cubic meter (Fig. 7*A*). The source of this population is somewhat uncertain, but, in view of the above-mentioned evidence of unsuccessful local production, it is believed that the adults consisted partly of members of the first brood of stock *C* from the eastern basin of the Gulf, and partly of the second brood of stock *A* from the outer Gulf (pp. 201–202). It is barely possible that propagation of this species is nowhere successful in the eastern Gulf and that all subsequent broods attributed to stock *C* were in reality migrants of stock *A*. This seems unlikely, however, since late nauplii off Mt. Desert in May (Fig. 6*B*) could hardly have been produced much farther away than the eastern basin.

By August further changes became evident. Eggs and early nauplii, presumably of the third brood of stock *C*, were concentrated in the Fundy region (Fig. 8*A* and *B*) and their scarcity or complete absence for some distance eastward from Mt. Desert would indicate that the depletion of the *P. minutus* population had now extended from the western Gulf to include the eastern basin. The similarity in the distribution of the two stocks, *B* (Fig. 8*C*) and *C* (Fig. 8*A* and *B*), in the Fundy region in August is most readily explainable on the basis that both were now centered in the same locality, and that the larvæ were derived from parents transported from the general vicinity of Georges Bank. Had observations been continued in September, it might have been possible to determine whether, with the decline of the predatory animal population, there occurred a progressive restocking to the westward in the inner Gulf by these migrants from offshore or their progeny. There is some indication that this may occur in Bigelow's (1926, p. 281) observation that there is "a greater absolute abundance over the area as a whole in late summer and autumn." Within the Bay of Fundy in mid-September, late nauplius stages of stock *C* (third brood) were most numerous (3,563 per cubic meter) in the entering drift from the Gulf and over the central basin.

Stock A.—Little can be said about the dispersal of this stock after April because of the probable confusion with stock *C* (p. 201). Originating offshore in March, by late April the larvæ, in late copepodite stages, were centered in the region of Georges and Browns Banks. Along the probable course of the drift smaller numbers had been dispersed to the outer part of the Bay of Fundy and along a tongue-like band penetrating the western area.

If copepodites in late June and August (p. 202) can be considered to consist in part of stock *A*, then this stock in the inner Gulf, at all times in the summer of 1932, remained restricted largely to the eastern basin and Bay of Fundy. One would have expected to find the progeny of the first brood (entering the western area in April) generally dis-

persed throughout the western Gulf, but the distribution of all copepodites in June (Fig. 9*A*) and again in mid-August (Fig. 9*B*) clearly indicated migration from the eastward.

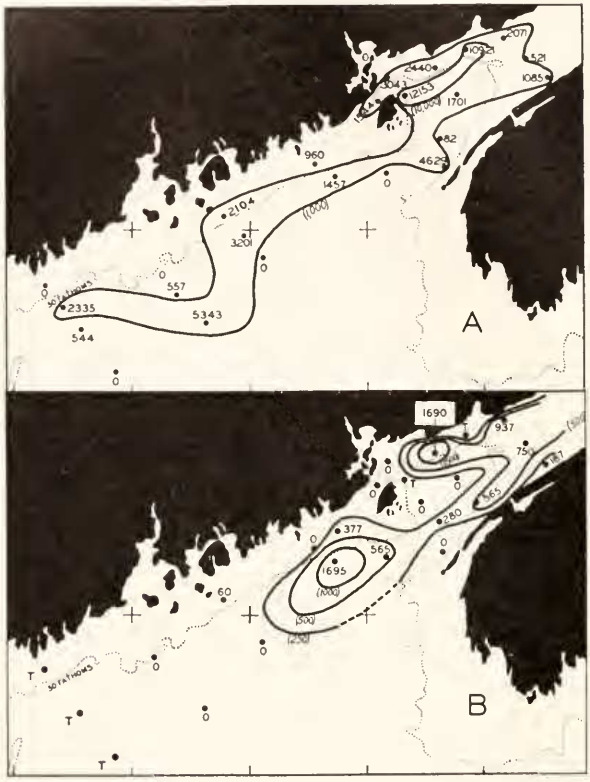

FIG. 9. Occurrence of late copepodite stages considered indicative of the outer Gulf stock in June (*A*) and August (*B*), 1932. June: number per minute of towing. August: number per cubic meter.

RELATIVE NUMERICAL STRENGTH OF PSEUDOCALANUS MINUTUS (ADULTS) IN THE ZOÖPLANKTON POPULATION

In the Gulf of Maine and Bay of Fundy *Pseudocalanus minutus* is second only in importance to *Calanus finmarchicus*. Offshore it is usually far outnumbered by the latter species, but in inshore waters such as the Quoddy region (Sta. 5, Table VI) and bays in the Gulf it is at times the dominant form. A similar condition is also found in the coastal region south of Cape Cod (Fish, 1925, p. 144, Fig. 45), and to the northward in the Gulf of St. Lawrence where Willey (1919, p. 187) found it constituting between 80 and 90 per cent of the copepod content between Prince Edward Island and the Magdalen Islands in May, 1915.

Combining the results of several years in the Gulf of Maine, Bigelow (1926, p. 282) found that *Pseudocalanus* averaged about 11 per cent of the copepod stock and as a rule was from one-tenth to one-fifth as abundant as *Calanus*. In 1932 during the period from April until September *Pseudocalanus* averaged 4.9 per cent of the total zoöplankton population of the Gulf, and *Calanus* 42.9 per cent, a ratio falling within Bigelow's range.

In the Bay of Fundy, based on monthly averages for three stations, the mean percentage of *Pseudocalanus* in meter net hauls for the year ending in August, 1932 was approximately 10, as shown in Table VI.

TABLE VI

1931–1932	*Pseudocalanus minutus*			
Month	Mean	Sta. 5	Sta. 6	Sta. 8A
September	2.3	3.7	2.8	0.5
October	1.5	1.5	——	——
November	1.9	2.1	3.3	0.3
December	3.1	4.5	2.3	2.5
January	8.2	8.2	——	——
March	12.0	6.6	10.9	18.5
April	5.8	5.5	5.8	6.0
May	22.0	53.2	8.0	4.8
June	43.4	83.2	45.2	1.7
July	3.0	3.0	——	——
August	5.3	15.2	0.8	0
Mean for Year	9.9	17.0	9.9	4.3

Along the New Brunswick shore (Station 5) it formed a much more important part of the plankton population than over the central basin or along the Nova Scotian side. Whereas *Calanus* increased in a seaward direction from the New Brunswick coast, the relative percentages of *Pseudocalanus* for the year decreased from 17 per cent in the Quoddy region to 4.3 per cent at the entrance to the Bay (Station 8*A*). This condition remained constant except for a short period following vernal augmentation when the percentage was greatest in the path of the drift from the Gulf. The highest value in the Bay (83.2 per cent) was found in the outer Quoddy region in June.

During the summer (April–September) the relative percentage of *Pseudocalanus* decreased westward from the Bay of Fundy, averaging 17.2 per cent in the Bay and as previously mentioned, 4.9 per cent in the Gulf, with minimum values in the western area.

Monthly averages indicated a definite seasonal variation in all areas covered in 1932 as the summer advanced. The highest value for the western area (10.6 per cent) was in April, for the central area (12.5 per cent) a month later in May, and for the New Brunswick area (59.2 per cent) in June. These results reflect the progressive response to vernal augmentation eastward along the coast. Indicating immigration from the western and outer Gulf, the Nova Scotian area yielded the highest percentages in March and April. Almost everywhere there was a continued decline after the first maximum, in spite of subsequent propagation.

The importance of *P. minutus* in the natural economy of the region is obviously greater than the relative numerical strength of the adult

TABLE VII

1932			Gulf of Maine			Bay of Fundy		
Cruise	Month	Total region	Total gulf	Western area	Central area	Total bay	New Brunswick area	Nova Scotian area
26	April	12.4	7.9	10.6	5.2	21.5	29.0	14.4
27	May	12.7	8.1	4.3	12.5	21.4	34.3	6.4
28	June	16.8	7.3	3.5	11.7	35.3	59.2	7.5
30	August	2.1	1.0	0.7	1.4	4.3	4.8	3.7
32	Sept.	1.3	0.1	0.3	T	3.6	2.1	5.1
Mean	April–Sept.	9.1	4.9	3.9	6.2	17.2	25.9	7.4

population would imply. Although, as Bigelow (1926, p. 282) has pointed out, the adult stock is still far behind *Calanus* because of its smaller size and fewer numbers, the enormous number of larvæ produced and subsequent rate of depletion indicate that its importance to those small predatory forms (including several of the more important species of Gulf fishes during their early existence) feeding on larval copepods must be considerably greater in some parts of the region than that of *Calanus*.

SUMMARY

1. *Pseudocalanus minutus* is generally distributed both in neritic and offshore waters. Having a somewhat greater thermal range it regularly outnumbers *Calanus* in neritic areas south of Cape Cod and on occasions in boreal waters also.

2. Propagation begins in March and continues in a succession of generations until September. It starts earlier in the southern part of the range where there are also a greater number of annual broods.

3. Eggs appearing at progressively later periods (approximately monthly intervals) in the outer Gulf, western area, and Bay of Fundy make possible a distinction of three major breeding stocks.

4. In the western stock there are at least three and possibly four breeding periods, March–April, May–June, July–August and September.

5. In the eastern stock there is evidence of three breeding periods, April–May, June–July, and August.

6. The outer Gulf stock is not clearly traceable due to probable overlapping of subsequent breeding periods with those of the eastern stock, but four periods are indicated.

7. There appears to be a developmental period of approximately two months throughout the region.

8. *Pseudocalanus* is very prolific and its early larvæ greatly outnumber those of *Calanus*. Mortality is relatively much higher in *Pseudocalanus*, the depletion being greatest in nauplius stages, although a second critical period during maturation is indicated.

9. There is no evidence of successful propagation in the Bay of Fundy, and the western area declines in importance after the first brood. Subsequent propagation of all breeding stocks appears to be centered in the outer Gulf.

10. The adult stock of *Pseudocalanus* is second only to that of *Calanus* in numerical importance, averaging 9.9 per cent of the total zoöplankton population in the Bay of Fundy during the year 1931–32 and 4.9 per cent of the summer population in the Gulf.

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